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PHRYMA LEPTOSTACHYA L., A MORPHOLOGICAL STUDY

THEO. HOLM

(WITH PLATES VIII–X)

At an early date placed as the sole member of "Ordo CXLVI: Phrymaceae,"[1] the monotypic genus *Phryma* has been regarded, nevertheless, as representing a mere tribe of the Verbenaceae by BENTHAM and HOOKER, and until very recently by all American authors. As may be seen from SCHAUER'S excellent description, the structure of the fruit ("caryopsideus monospermus") and of the seed ("exalbuminosum, embryon rectum, radicula supera cet."), besides the peculiar calyx ("superiore [labio] tripartito laciniis subulatis apice reduncis, inferiore [labio] brevissimo bifido"), these characters are much too distinct for admitting the genus among Verbenaceae, even as an anomalous genus. For many years the family Phrymaceae was thus ignored, until it became reestablished by BRIQUET[2] in a paper dealing with the anatomy of Phrymaceae, Stilboideae, Chloanthoideae, etc.; and further, in the treatment by this same author in ENGLER and PRANTL'S *Natürliche Pflanzenfamilien*.

Only one species is known, *P. leptostachya* L., but a few varieties have been described by BRIQUET. These are *parvifolia* (Rafin.) Briq., from the Allegheny Mountains, and preserved in the herbarium of DELESSERT; *inciso-crenata* Briq., cultivated in the garden of Ventenat; and *lanceolata* Briq., from Arkansas and Pennsylvania. The geographical distribution is quite remarkable, the species occurring in Canada (New Brunswick, Ontario), in the Atlantic States southward to Florida, and also in the Himalayas and in Japan; the variety *lanceolata* occurs with the type in Japan.

Notwithstanding the fact that the internal structure, of the mature plant only, has been described by BRIQUET, there are still some points worthy of consideration drawn from the seedling and compared with the mature stage. Moreover, the origin of the secondary tissues in the stem deserve attention, besides the general structure of the root system.

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[1] SCHAUER, J. C., in DE CANDOLLE'S Prodromus **11**:520. 1847.

[2] BRIQUET, J. I., Mém. Soc. Phys. et Hist. Nat. Genève **32**:1894–97.

The seedling

In its native haunts seedlings of *Phryma* are difficult to be found. Being a truly sciaphilous plant and developing only a small number of seeds in proportion to the size of the plant, *Phryma* depends on dispersing its seeds, or better the fruits, by animals. The long, slender teeth of the persistent calyx are hooked at the tip, and are likely to adhere to fleece and clothing like a bur. Thus the fruits become scattered, and the seedlings are so very much like those of other sylvan types with opposite leaves that they may be mistaken for entirely different genera, of Labiatae and Compositae, for instance, when their cotyledons have dropped.

Fig. 1 represents the seedling (natural size) of *P. leptostachya*, and it is noticed at once that the cotyledons are hypogeic, and that they remain inclosed within the seed, surrounded by the thin pericarp. There is only a very short hypocotyl, and the primary root (*R*) is relatively short; a much longer secondary root (*r*) soon develops from beneath the insertion of the cotyledons and between them, as may be seen in fig. 2 (*r*). In the axils of the cotyledons buds are already visible at this very young stage (*B* in fig. 2), but they remain dormant during the first season. The aerial shoot of the seedling consists of a long, cylindric, glabrous, and erect epicotyl (*Ep.* in fig. 1), and a few short pubescent internodes with leaves of approximately the same outline as those of the mature plant. Characteristic of the seedling of *Phryma*, therefore, are the hypogeic cotyledons, the long epicotyl, and the early development of a secondary root, exceeding the primary in length and thickness. By this structure the seedling is easily distinguished from the corresponding stage of most of the other sylvan types with opposite leaves; for in the Compositae, for instance, the cotyledons are epigeic; and among the Labiatae, *Collinsonia*[3] is the only North American genus known to germinate with hypogeic cotyledons. As for the seedlings of the Verbenaceae, the cotyledons are epigeic in the genera examined by LUBBOCK[4] (*Verbena*, *Lippia*, *Clerodendron*, *Callicarpa*, *Stachytarpheta*, and *Rhaphithamnus*).

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[3] Compare Medicinal plants of North America. Merck's Report. New York. April 1909.

The subterranean organs of the mature plant

An examination of the subterranean portion of the mature plant (fig. 3) shows that the primary root has faded away completely, but is replaced by several strong secondary roots, which are brownish, somewhat fleshy in texture, and which traverse the ground horizontally, all developed from the lowermost, very short internode of the floral shoot. Furthermore, the presence of several axillary buds (*B*) is observed, covered with opposite, scalelike leaves; one of these buds is much larger than the others, and from this a new floral stem will be produced during the following season. The subterranean stem portion of *Phryma* thus merely represents a pseudo-rhizome with a few short, persistent internodes, a few over-wintering buds, and a secondary system of roots. Similar to the seedling, the aerial shoot of the mature plant commences with a long internode preceding a few shorter ones, terminated by the long, very slender, loosely flowered spike. There is, therefore, a great resemblance between the habit of the seedling and that of the mature plant, with the exception of the early disappearance of the primary root in the latter.

The root

None of the roots, neither the primary root nor any of the secondary roots of the seedling or of the mature plant, contain fungal hyphae, otherwise not infrequent in plants growing in shady localities; and in none of the roots was secondary increase to be traced beyond the stele. Root hairs abound, and a distinct exodermis with the cell walls suberized, and with foldings on the radial walls, was observed in the secondary roots, but not in the primary. The cortical parenchyma is homogeneous, compact, filled with starch in the secondary roots only. The endodermis is thin-walled, and the pericambium consists of a single stratum with no indication of developing cork or secondary cortex. But inside the pericambium the stele soon increases in thickness in the usual way, and already at the seedling stage. While no pith was observed in the primary root, this tissue is well represented in all the secondary roots, attains quite a considerable width in mature specimens, and contains deposits of starch.

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[4] Contribution to our knowledge of seedlings. London. 1892 (p. 367).

We have thus in *Phryma* two very distinct types of roots: nutritive roots, represented by the primary root; and a combination of contractile and storage roots, as shown by the secondary roots with contractile exodermis and starch deposits in cortex and pith.

The aerial stem

In seedlings and in young, purely vegetative shoots the internodes are cylindric, while in mature plants the stem becomes obtusely quadrangular and bisulcate to sharply 4-winged between the flowers. Furthermore, the internodes, at least in mature specimens, are more or less nodose, the node appearing some distance from the insertion of the leaves; these nodes are generally purplish, while the other parts of the stem are green. Similar nodes occur in various other plants, as among Labiatae, Scrophulariaceae, Polygonaceae, Acanthaceae, Caryophyllaceae, etc., and they may be located either directly at the insertion of the leaves or some distance therefrom. According to RÜTZOU,[5] the structure of the nodes in these families differs from that of the slender portion by the presence of more collenchyma, and of a less developed stereome; this author explains the function of these nodes to consist in facilitating the bending of the stem, when such is necessary. In *Phryma*, however, the internal structure is almost identical throughout the internode, including the swelling, but the function seems to be the same as observed by RÜTZOU.

The stem structure of *Phryma* in general is very uniform in young as well as in mature specimens, in the basal as well as in the apical internodes. The cuticle is thin and smooth in the subterranean stem portions, but becomes gradually thicker and longitudinally wrinkled in the internodes above. The epidermis is thin-walled, and shows two types of hairs, pointed and glandular. The pointed hairs consist of a few cells in one row, covered with a granular cuticle; while the glandular hairs have a two-celled head borne on a single foot-cell, or on a long stalk of several cells in a single row; the sessile glandular hairs are especially frequent on the basal internodes, while the long-stalked hairs abound in the inflorescence. The pointed hairs are frequently curved to almost hooked, and occur especially on the upper internodes. Within the epidermis are a few (one or two) continuous strata of collenchyma, but only in the aerial internodes, not in the subterranean. The cortical parenchyma attains its greatest width in the short internodes of the pseudo-rhizome, where it consists of about 20 thin-walled compact layers; no crystals and no deposits of starch were observed in any part of the cortex.

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[5] Bot. Tidsskr. Kjbhvn **12**:248. 1880–1881.

The endodermis is present throughout the stem, but it is not always distinct, since the Casparyan spots are sometimes difficult to detect; besides, the individual cells are uniformly thin-walled, and of the same shape and lumen as the adjoining cortical parenchyma; moreover, the endodermis does not contain starch.

Bordering on the inner face of the endodermis is the so-called pericycle, relatively poorly developed in *Phryma;* as a closed sheath of stereids this tissue occurs only in the inflorescence, when the fruits have matured; in the pseudo-rhizome it is represented merely by parenchyma with isolated strands of stereome; while in the other internodes it is either uniformly thin-walled or interspersed with a few stereids, but with no regularity.

The herbaceous stem of *Phryma* does not increase much in thickness, and beyond the formation of secondary mestome strands no other secondary tissues were observed. The primary mestome strands are thus readily visible in all the internodes, and they are strictly collateral; there are 6 in the cylindric epicotyl of the seedling, and they are arranged in two broad groups; in the mature plant the mestome strands constitute 4 broad strands, one in each angle of the quadrangular stele. These primary strands contain leptome, cambium, and short rays of hadrome, in which the young vessels, reticulated and scalariform, are much wider than the primordial, spiral and annular. An endoxyle (fig. 7) is quite well represented, especially in the subterranean internodes as well as in the swollen portion of the upper internodes. Between these primary mestome strands in the various stem portions (of seedlings and mature individuals) there are several strata of secondary mestome, that is, leptome and thick-walled libriform, but with no vessels.[6]

It is interesting to trace the origin of these tissues, the leptome and the libriform, and it might be stated at once that only the leptome develops from the pericycle, and only sometimes. What seems to be more important for the development of these secondary tissues in *Phryma* is undoubtedly the peripheral portion of the primary parenchymatic or medullary rays, which is still meristematic and capable of producing new tissues. Fig. 8 shows a small part of the interfascicular tissue, taken from the base of a very young lateral inflorescence, and here may be seen the thin-walled, large-celled endodermis (*End*), inside of which are small strands of young leptome, some perhaps developed from the pericycle itself, while others have developed in the tissue inside, the primary parenchymatic ray. As may be readily seen from this drawing, there is no real indication of any definite sheath such as a pericycle of one or of several strata. There is, on the other hand, a very distinct meristematic tissue in the periphery of the primary parenchymatic (medullary) ray giving rise to leptome, sometimes bordering on the endodermis, or some distance from it. In other words, this particular section (fig. 8) does not show the derivation of the secondary leptome from the pericycle alone, but from a meristematic tissue within the endodermis, a tissue of several homogeneous strata.

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[6] SANIO (Bot. Zeit. 1863:101) proposed the term "libriform": "einfache (d. h. ungetheilte) bastartige Holzfasern oder Holzzellen, fibrae sive cellulae libriformes simplices. Um einen kurzen Ausdruck zu gewinnen werde ich dieselben Libriformfasern, und das daraus bestehende Gewebe Libriform nennen." HABERLANDT (Physiol. Pflanzenanat. 1896:138), however, calls attention to the fact that the distinction between libriform and stereome depends upon the different location of these tissues, and more so than in respect to their structure. SANIO'S "libriform" applies to the stereids in the hadrome, and it is customary, therefore, to use this term for mechanical cells (stereids) that are developed inside the cambium, and stereome for those outside. However, from a physiological point of view, it seems unimportant whether such mechanical cells are located inside or outside the cambial zone, hence the distinction between libriform and stereome is not well founded except topographically.

In the internodes of the seedling, this structure, as described above, occurs in the apical internode, and with no indication, so far, of any development of secondary hadrome inside the leptome. To trace this, the origin of the secondary hadrome, we must examine the next internode, the one below the apical, shown in fig. 9. Here are seen the innermost strata of the cortex (*C*) and the endodermis (*End*); also, on the left side of the section, a part of one of the primary mestome strands (*M*) has been drawn, consisting of leptome (*L*) and a short ray of vessels. The broad interfascicular tissue consists, on the other hand, only of several well defined leptomatic strands, and of a tangential cell-division within the large, thin-walled parenchyma inside the leptome. There is actually no indication of any distinct pericycle in this section either, but there is certainly a very pronounced indication of the presence of a meristem in the periphery of the primary parenchymatic (medullary) ray. The result of these tangential cell-divisions within the leptome may be seen in fig. 10, which has been drawn from the epicotyl of the seedling. It consists of the development of thick-walled libriform in such a way that the innermost tangential cell wall becomes lignified, and very rapidly so, while the outermost is still meristematic, so as to give rise to another libriform cell in the same radius as the first developed. There is no distinct ring of cambium, therefore, since the innermost cell wall of each cell, which divides tangentially, becomes lignified almost at once, while the outermost remains active so as to yield another cell to the secondary hadrome, and always in the same radius.

In comparing the structure of these internodes of the seedling with that of an old internode of a mature specimen, which is drawn in fig. 15, we notice the continued growth of the interfascicular hadrome (*H*) as many radial layers of thick-walled libriform, while the leptomatic strands are about the same, and located in thin-walled parenchyma; no pericyclic sheath seems to be differentiated in this section either. This internode (fig. 15) was from the aerial portion of the stem, and examining the structure of the pseudo-rhizome, we notice a marked difference (fig. 16) consisting in the development of a partly stereomatic pericycle outside the primary mestome strands (*s* in fig. 16). As shown in this figure, there are two thin-walled, parenchymatic strata between the endodermis (*End*) and the leptome (*L*), interspersed with stereids, and these two strata evidently represent what various authors have interpreted as a heterogeneous pericycle. Still another structure of this same pericycle may be observed in the oldest internodes of the inflorescence, that is to say, when the fruits have matured; in these there is a very distinct sheath of two layers of stereids surrounding the leptome, hence representing a homogeneous, in this case a purely stereomatic, pericycle.

The stereids inside the endodermis are thus only visible in the old, subterranean internodes of the main stem, and in the oldest internodes of the inflorescence, when the fruits have matured. But in all the other internodes, whether of seedlings or of mature plants, there is no pericyclic stereome, and barely any indication of a parenchymatic pericycle either. Moreover, the origin of the secondary mestome strands in *Phryma* cannot be attributed to the activity of a pericycle, but, as has been demonstrated, these secondary strands of leptome and thick-walled libriform arise from the meristematic, peripheral strata of the primary parenchymatic (medullary) rays.

Inasmuch as the origin of the secondary mestome strands, or, to be more exact, the interfascicular strands, seems to be different when we compare a number of dicotyledonous, especially herbaceous, stems, it might be appropriate to present a brief abstract of the history of the pericycle. The term "pericycle" was proposed by VAN TIEGHEM[7] and applied to the parenchyma, of one or several layers, which he found in the stem between the endodermis and the mestome strands, as well as in the roots between the endodermis and the outer face of the leptome, and between the endodermis and the protohadrome vessels. To the activity of the pericycle VAN TIEGHEM ascribed the origin of the interfascicular arches of cambium with the subsequent development of secondary mestome strands. MOROT,[8] in describing the pericycle in general, calls attention to the fact that while the pericycle is always present in roots (frequently called pericambium), it is not always to be found in stems; on the other hand, he agrees with VAN TIEGHEM in respect to the function of the pericycle. GÉRARD[9] and HÉRAIL[10] question the assertion of VAN TIEGHEM in respect to the function of the pericycle in stems, and describe a number of cases where the interfascicular tissues develop independently of the pericycle. Moreover, HÉRAIL describes some cases of secondary mestome developing in the pith (Melastomaceae and Campanulaceae). Finally, HABERLANDT[11] makes no use of the term pericycle in stems, but only in roots; and in reference to the secondary increase in stems, he speaks of a "cambium ring" being the direct product of a "procambium," and of an interfascicular cambium owing its existence to a meristem in the primary parenchymatic (medullary) rays.

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[7] Sur quelques points de l'anatomie des Cucurbitacées. Bull. Soc. Bot. France **29**:280. 1882.

[8] Recherches sur le péricycle ou couche péripherique du cylindre central chez les Phanérogames. Ann. Sci. Nat. Bot. VI. **20**:249. 1885.

In *Phryma* the presence of stereids is actually the only distinct indication of a pericycle, as scattered strands in the pseudorhizome, or as a closed sheath in parts of the inflorescence. The origin of these stereids I have been unable to detect, but it may be sought in the outermost layers of the leptome, and rather so than in any particular tissue, such as a pericycle for instance, inside the endodermis. Therefore, I am most inclined to believe that *Phryma* lacks a pericycle; in any case, the interfascicular tissues appear to develop independently of it, especially the libriform. However, the term "pericyclic" is quite convenient to use when describing the stereome strands between the endodermis and the leptome, because they are "peri" "cyclic," even if we do not always regard them as representing a pericycle as defined by VAN TIEGHEM, that is, a constant sheath of parenchyma from which the secondary tissues arise. It seems also worth while to compare this pericycle of stems with the well known pericambium of roots, where it represents the peripheral tissue of the stele, and typically so.

Returning to the stem of *Phryma*, the central part of the stele is occupied by a broad, thin-walled pith, which is hollow in aerial internodes, but solid in the subterranean internodes, where it contains deposits of starch, but no crystals. As mentioned above, the nodes show no other modification of structure than an enlargement of the parenchymatic tissues, cortex and pith; partly also of the hypodermal collenchyma; furthermore, in these nodes the pericycle is very incomplete and without stereids; also the development of libriform goes on more slowly, so that several strata of cambium may be observed between the primary mestome strands.

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[9] Passage de la racine à la tige. Ann. Sci. Nat. Bot. VI. **15**:1881.

[10] Recherches sur l'anatomie comparée de la tige des Dicotylédones. Ann. Sci. Nat. Bot. VII. **2**:1885.

[11] Physiologische Pflanzenanatomie. Leipzig. 1896.

The leaf

As indicated by the varieties described by BRIQUET, the foliage of *Phryma* exhibits several quite distinct forms, some of which may be found on the same plant, if we examine the leaf-pairs from the basal to the apical internodes of seedlings as well as of adult specimens. The leaf is described by GRAY[12] as "ovate, acuminate, coarsely serrate." A little more is given by TORREY,[13] who calls them ovate, but distinguishes between the lower ones ("abruptly narrowed at the base, and furnished with long petioles") and the upper ones ("nearly or quite sessile"). SCHAUER describes the leaves as "ovato-oblonga, in petiolum longum attenuata, acuminata, grosse crenato-serrata"; and finally, the Himalayan plant is said by HOOKER[14] to have "ovate or ovate-lanceolate" leaves. As may be seen from the drawing of the seedling (fig. 1), the shape of the lowermost leaf-pair is broadly ovate and abruptly narrowed at the base, while the leaves above are elliptic. In fig. 4 I have drawn a leaf of a specimen from the mountains of Virginia, and the entire foliage of this specimen showed this same outline. Fig. 5 shows a leaf of a specimen from Ohio, in which the uppermost three pairs showed this outline, while the basal pairs were much broader. Finally, fig. 6 shows a leaf of a Japanese specimen, in which all the leaves were ovate and with the margin crenulate. Among some other specimens examined, I found the upper leaves of a specimen from Nippon elliptic, while the lower ones were ovate-oblong; all the leaves of a specimen from Kansas were lanceolate; while all the leaves of a plant from Georgia were ovate. The leaf margin was observed to vary to the same extent from crenate to serrate, even on the same individual. It is thus somewhat difficult to define the typical leaf-form in *Phryma;* it varies much, but the ovate outline may be the fundamental one.

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[12] Synoptical flora of North America. Second Edition. **2¹**:334. 1886.

[13] Natural history of New York. 1843 (p. 53).

[14] Flora of British India **4**:561. 1885.

The internal structure is bifacial, the stomata being confined to the dorsal face, and the chlorenchyma being differentiated into a ventral palisade tissue and a dorsal pneumatic tissue. On both faces of the blade the cuticle is thin and smooth except above and below the veins, where it is wrinkled. The epidermis is a little thick-walled where it covers the veins, and the cell-lumen is somewhat wider on the ventral face than on the dorsal (fig. 17). Viewed in superficial sections, the lateral cell walls of the epidermis are undulate on both faces of the blade, and the stomata lack subsidiary cells. Short, almost sessile, glandular hairs (figs. 12, 13) abound on both faces of the leaf, and, as may be seen from the drawings, the head is two-celled. Besides these glandular hairs there are also, and especially on the ventral face, some long, pointed, multicellular hairs (in one row) with cuticular pearls. The chlorenchyma consists of a single layer of very short and plump palisade cells (*P* in fig. 17) covering three strata of an open pneumatic tissue (P^+ in fig. 17): in superficial sections this pneumatic tissue shows intercellular spaces of considerable width (fig. 18).

The mechanical tissues are poorly represented, there being only a few hypodermal layers of collenchyma above and below the midrib and the secondaries, and also the leptome of the midrib is supported by an arch of thin-walled stereome (*S* in fig. 19). A broad, thin-walled water-storage tissue surrounds the midrib, but there is no endodermis; the lateral veins, on the other hand, are surrounded by green parenchyma sheaths (fig. 17). All the mestome strands are collateral, and the median is the broadest. The petiole, when examined just beneath the blade, shows exactly the same structure as the midrib, except that it contains two very thin mestome strands, one on each side of the median. Finally, it may be mentioned that the throat of the corolla of the flower is not naked as stated by SCHAUER, but covered with numerous hairs, glandular (fig. 11) as well as pointed (fig. 14).

Summary

Phryma represents a sciaphilous type, well marked by the structure of the ample leaf blade, with low palisade cells and very open pneumatic tissue; also by the poor development of the mechanical tissues in the stem as well as in the leaf. The vegetative reproduction is confined to the few buds on the short pseudo-rhizome, and the roots produce no shoots. For dispersing the seeds the plant is well equipped by the hooked teeth of the persistent, reflexed calyx.

BROOKLAND, DISTRICT OF COLUMBIA

EXPLANATION OF PLATES VIII–X

FIG. 1.—Seedling of *Phryma leptostachya:* the dotted line indicates the surface of the soil; *Ep*, epicotyl; *Cot*, the achene with inclosed cotyledons; *H*, hypocotyl; *R*, primary root; *r*, secondary root; natural size.

FIG. 2.—Basal portion of same seedling: *B*, buds in the axils of cotyledons; other letters as above; magnified.

FIG. 3.—The pseudo-rhizome of a mature specimen: *S*, base of stem; *B*, bud which will produce a floral shoot in the following year; ×2.

FIG. 4.—Leaf of a specimen from Virginia: two-thirds natural size.

FIG. 5.—Leaf of a specimen from Ohio: two-thirds natural size.

FIG. 6.—Leaf of a specimen from Japan: two-thirds natural size.

FIG. 7.—Cross-section of a subterranean internode showing the endoxyle; ×480.

FIG. 8.—Cross-section of the basal internode of a lateral inflorescence: *End*, endodermis; *L*, secondary leptome; ×744.

FIG. 9.—Cross-section of one of the apical internodes of the seedling: *C*, cortex; *M*, hadrome of a primary mestome strand; *P*, pith; other letters as above; ×744.

FIG. 10.—Cross-section of the epicotyl of a seedling: *L* and *H*, interfascicular leptome and libriform; other letters as above; ×744.

FIG. 11.—Glandular hair from the throat of the corolla; ×600.

FIG. 12.—Glandular hairs from the leaf; ×600.

FIG. 13.—Same; ×600.

FIG. 14.—Pointed hair from the throat of the corolla; ×600.

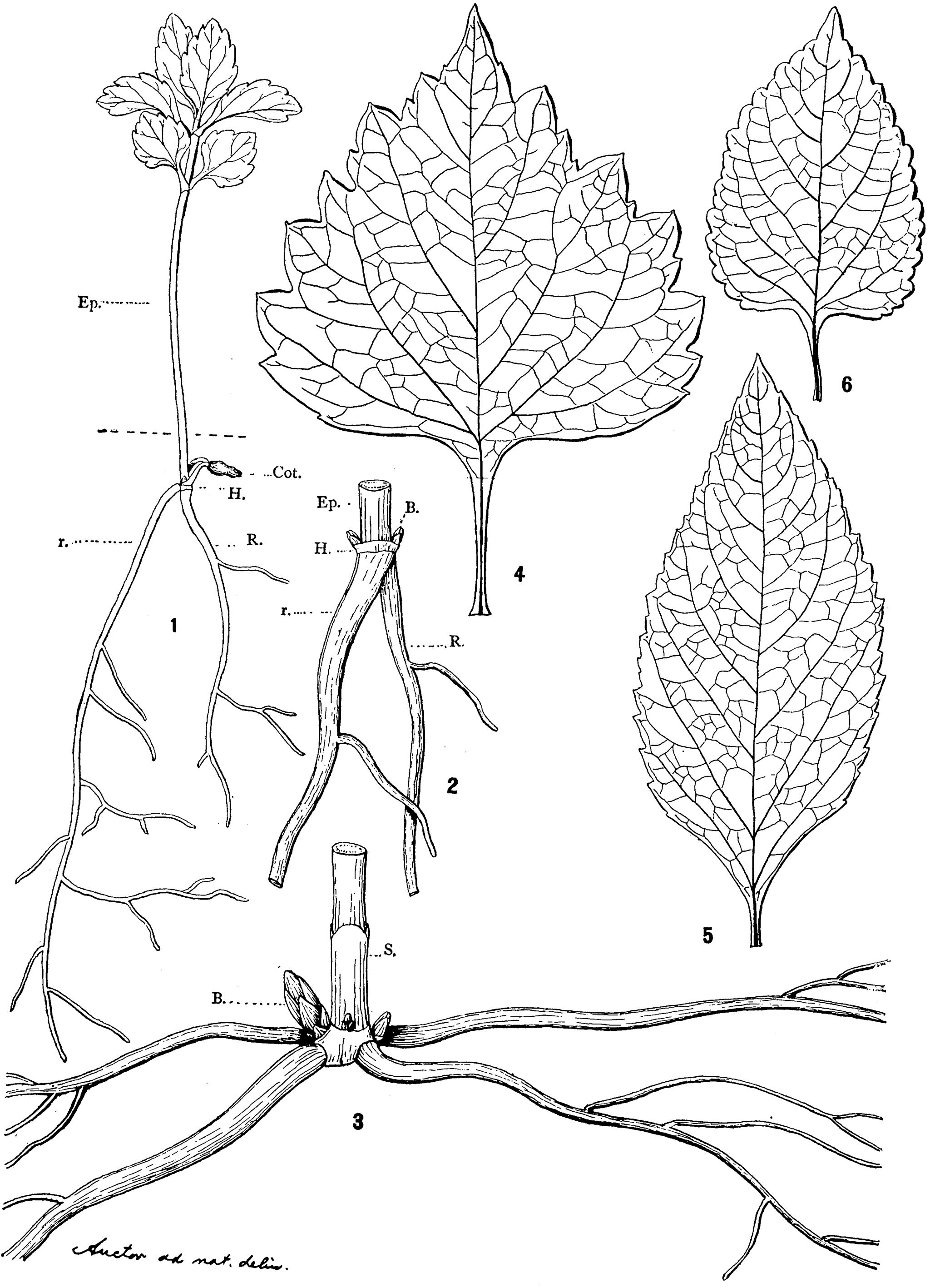
FIG. 15.—Cross-section of an old internode of a mature specimen: *L* and *H*, interfascicular leptome and libriform; the other letters as above; ×600.

FIG. 16.—Cross-section of a subterranean internode of a mature specimen: *S*, stereomatic pericycle; *Camb*, cambium; other letters as above; ×744.

FIG. 17.—Cross-section of lateral part of leaf blade: *Ep*, ventral epidermis; *Ep*+, dorsal epidermis; *P*, palisade tissue; *P*+, pneumatic tissue; ×600.

FIG. 18.—Pneumatic tissue of leaf, superficial section; ×360.

FIG. 19.—Cross-section of part of midrib of leaf: *S*, stereome; *L*, leptome; *H*, hadrome; ×600.



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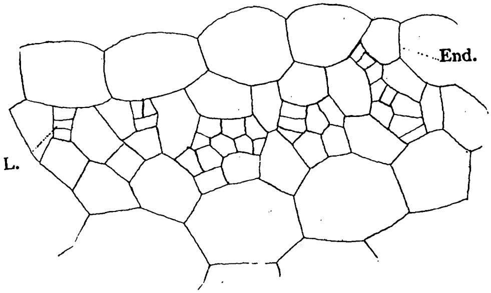

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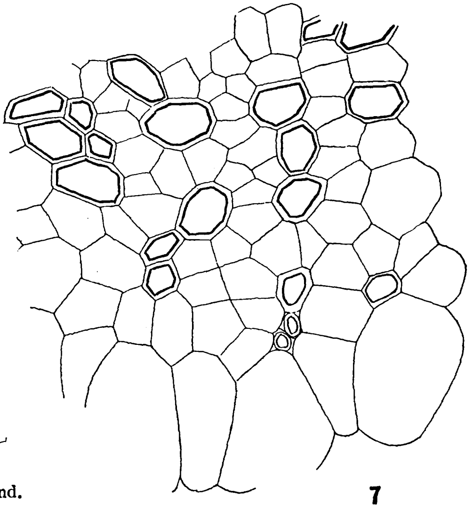

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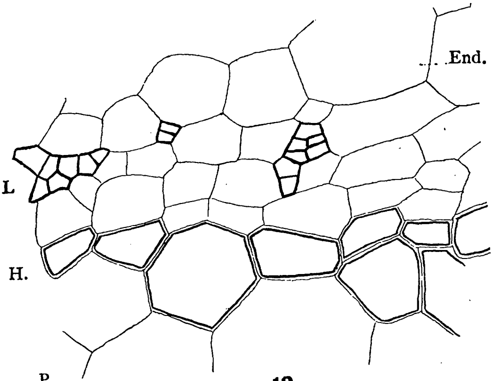

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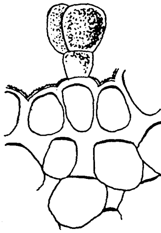

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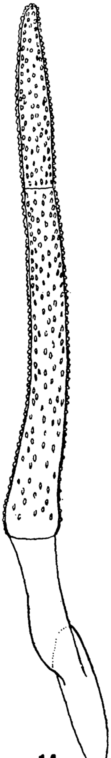

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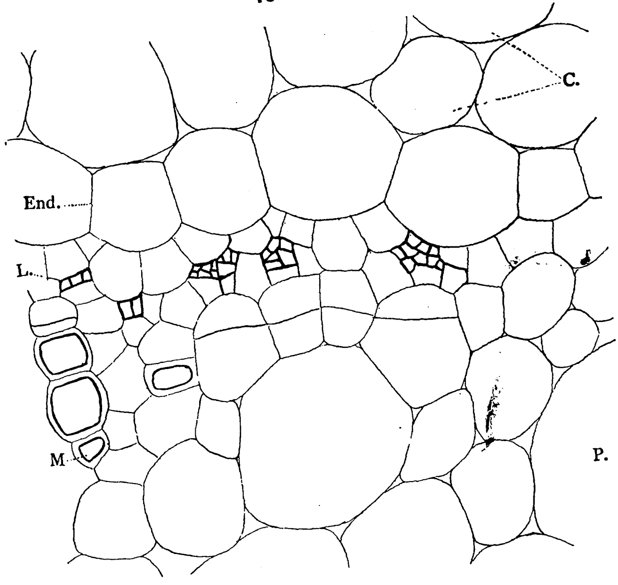

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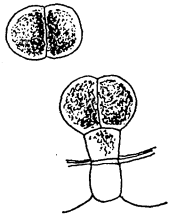

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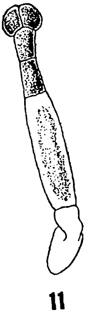

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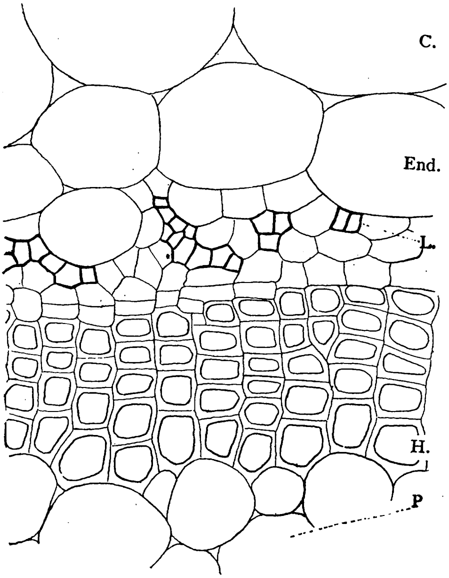

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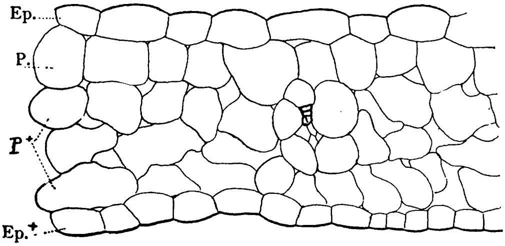

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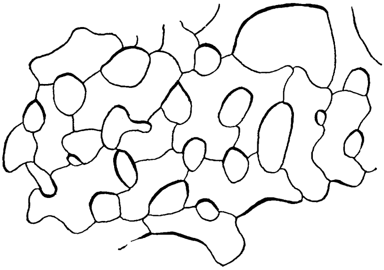

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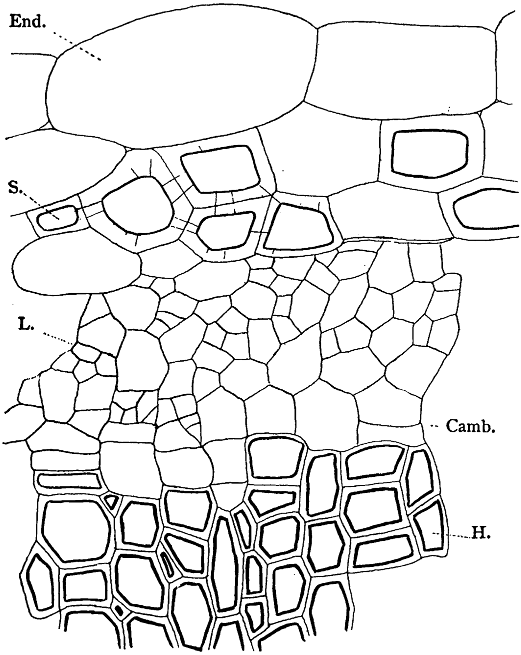

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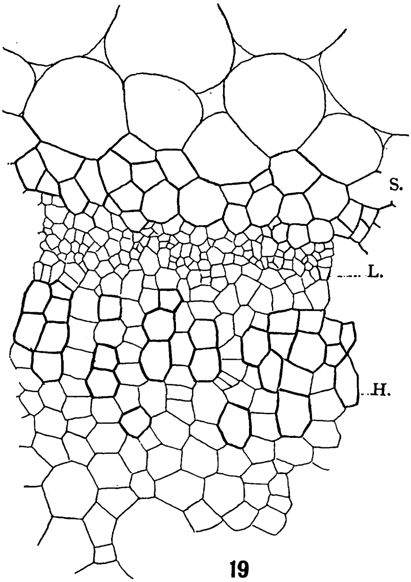

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HOLM on PHRYMA